BIOGEOGRAPHICAL AND ECOLOGICAL LIMITS OF NEW WORLD PASSALIDAE (COLEOPTERA)[1]

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ABSTRACT

In the New World, beetles of the primarily tropical family Passalidae occur in rotting wood from southern Michigan and southern Ontario to northern Argentina, Paraguay, Uruguay, and southern Brazil. They are found in the West Indies, Isla del Coco, and Galapagos Islands. They are not known from the forests of southern Chile or the Pacific North-West, except for the only known fossil of the family from the Oligocene of Oregon. A few species, mostly Proculini, are encountered above 2800 m elevation. The most widely distributed species are those of the tropical lowlands below 1500 m. Most species occur in moist forests, though some species occur in dry forests and even in nests of desert ants. Most species live in hardwood but some are found in conifers and a few in palms. Passalids are occasionally found in other microhabitats, possibly including limestone caves inhabited by oilbirds. New records are cited for various species from Peru, Costa Rica, Belize, Mexico, Trinidad, and Grenada.

RESUMEN

Coleópteros de la familia tropical Passalidae viven en la madera podrida desde el sur de Míchigan y Ontario hasta el norte de Argentina, Paraguay, Uruguay, y el sur de Brasil. También, se encuentran en las Indias Occidentales, la Isla del Coco, y las Islas Galápagos. No se conocen en los bosques del sur de Chile ni el nordoeste de Norteàmérica, con la excepción del único fósil conocido de la familia, del Oligoceno de Oregon. Pocas especies, principalmente Proculini, se distribuyen por arriba de 2800 m de altitud. Las especies con mas amplia distribución son aquellas de las tierras bajas tropicales a altitudes inferiores a los 1500 m. El mayor número de especies ocurre en los bosques húmedos, aunque unas especies viven en los bosques secos y aún en los nidos de hormigas subdesérticas. La gran mayoría de las especies viven en la madera de dicotiledones aunque algunas se encuentran en coníferas y unas cuantas en palmeras. Ocasionalmente, los pasálidos se encuentran en otros microhabitats, entre estos se incluye muy posiblemente las cuevas calcáreas en donde vive el guácharo (*Steatornis caripensis* Humboldt). Se citan varias especies como nuevos registros para Perú, Costa Rica, Belice, México, Trinidad, y Grenada.

The primarily pan-tropical family Passalidae contains approximately 500 species. Apparently all live in rotting wood, though individuals may be found occasionally in other microhabitats. According to the most recent taxonomic revision (Reyes-Castillo 1970), the family contains 2 subfamilies. Only Passalinae occurs in the New World where it is represented by 2 tribes, the Passalini which is pan-tropical and the Proculini which is

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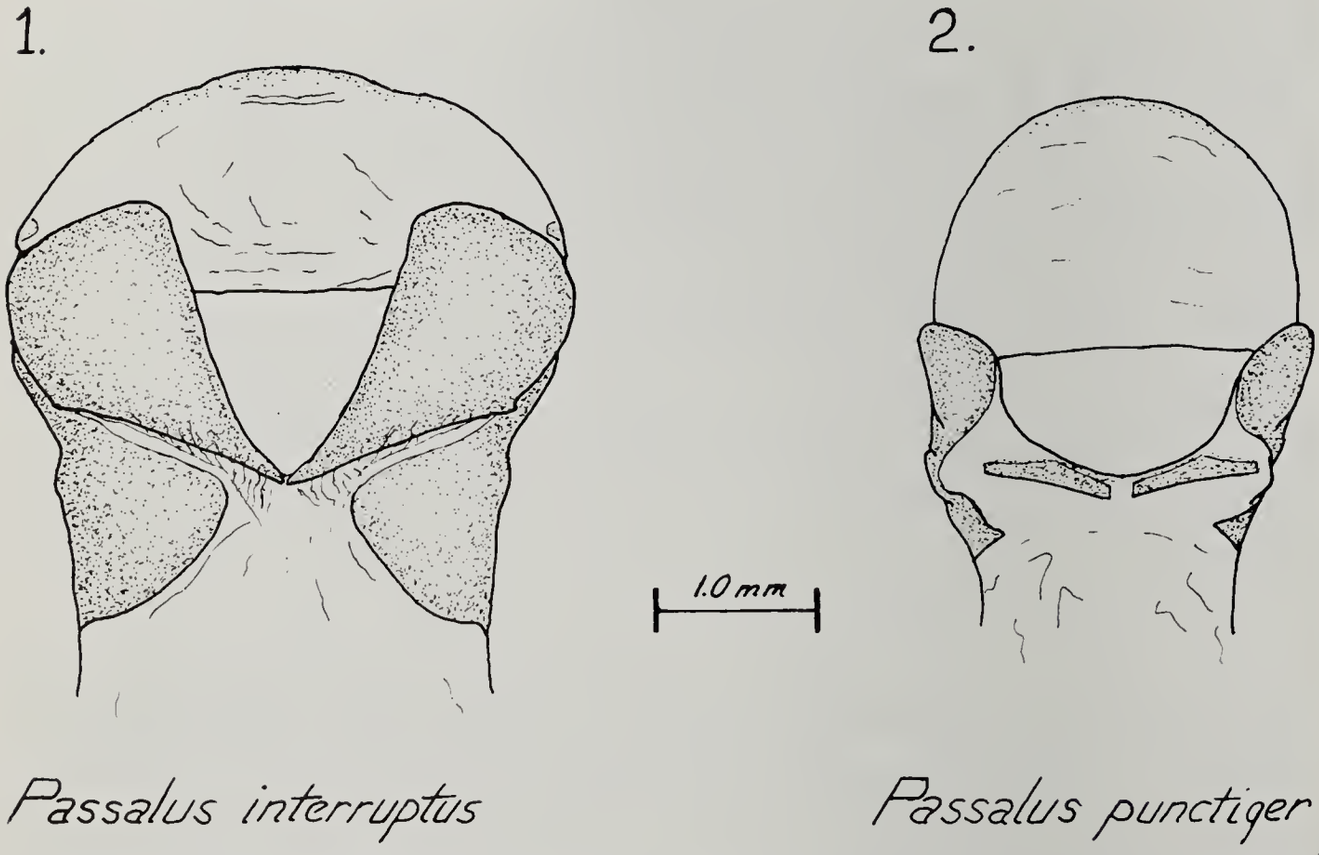
Neotropical except for *Odontotaenius disjunctus* (Illiger), formerly known as *Passalus cornutus* Fabricius or *Popilius disjunctus* Illiger.

The northern-most record I have found for any passalid is of *O. disjunctus* in Saginaw Co., Michigan. The southern-most record is of *Pharochilus politus* (Burm.), which occurs in Tasmania (Dibb 1938). A number of species are found in northern Argentina (Bruch 1942), Uruguay, Paraguay, and southern Brazil (Reyes-Castillo 1970). The southern-most verified New World record is for *Passalus punctiger* Lepeletier et Serville from Buenos Aires, Argentina (Reyes-Castillo pers. comm., 1976). I examined temperate forests in Chile and found no evidence of Passalidae; nor have I seen museum specimens from Chile. The record of *Passalus convexus* Dalman from Chile (Luederwaldt 1931) is probably erroneous. The forests of southern Chile, as well as those of the Pacific Northwest of the United States, lack passalids and are separated from the nearest passalid populations by extensive dry regions. Passalids may never have inhabited Chile; however, the only fossil known for the family is from the Oligocene of Oregon (Chaney 1927), confirmed as a *Passalus* by Reyes-Castillo (1976a). The New World passalid fauna extends into the Pacific with *Popilius lenzi* Kuwert on Costa Rica's Isla del Coco (Van Doesburg 1953) and *Passalus interruptus* (L.) in the Galapagos Islands (Van Dyke 1953). Only the Passalini are represented in the West Indies (Reyes-Castillo 1970).

Most species within the tribe Proculini occur in the mountains of Mesoamerica and northern South America, whereas the greatest diversity of New World Passalini is found in South America.



Figs. 1 & 2, Aedeagi of *Passalus*, dorsal view: 1, *P. interruptus*, Peru, San Martín Dept., near Tocache; 2, *P. punctiger*, Mexico, Tamaulipas, Gómez Farías.

Although Blackwelder (1944) lists the familiar *Odontotaenius disjunctus* as occurring as far south as Brazil, its range is actually Ontario, Canada, and the eastern United States (Reyes-Castillo 1970, 1973). In the United States, it occurs north to Massachusetts and Michigan, south to central Florida and west to Kansas and north-eastern Texas. Reyes-Castillo and I have examined many of the world's major collections and have collected in most of the countries from which it has been cited but have yet to encounter a specimen from outside this range.

Blackwelder (1944) lists 2 other species, *Passalus punctiger* and *P. interruptus,* as occurring in southern Texas. Reyes-Castillo (1973) considers *P. interruptus* as probably confined to Scuth America. Despite extensive collecting, we have not collected *P. interruptus* in Central America or Mexico. The many *P. interruptus* citations from this region have probably been caused by specimens of *P. punctiger* incorrectly identified as *P. interruptus.* Reyes-Castillo (1973) discusses the similarities between these species and reviews their taxonomic literature. Little attention has been paid, however, to the structure of the aedeagus. Specimens of *P. interruptus* I have examined from Peru and Trinidad have a very wide aedeagus, easily distinguishable from the narrower aedeagus I have seen in specimens of *P. punctiger* from the same areas as well as Colombia, Ecuador, Panama, Costa Rica, Guatemala, and Mexico (Figs. 1 and 2). The Trinidad record for *P. interruptus* is new in the sense that previous records (Reyes-Castillo 1973) state only that it is known from the Antilles.

Though I have not seen any specimens of *P. punctiger* collected in the U.S., it is possible that the species occurs (occurred?) in southern Texas. I have collected it some 275 miles south of the Texas border in Gomez Farías, Tamaulipas. This area is the northern-most extension of the lowland tropical deciduous forest in eastern Mexico (map, U. of California). At least 5 other species, however, occur further north. I collected *Odontotaenius striatopunctatus* (Percheron) and undescribed species of both *Petrejoides* and *Heliscus* in an oakpine forest south of Monterrey, Nuevo Leon, about 100 miles from the Texas border. On the west coast of Mexico, *P. punctatostriatus* (Percheron) and *Ptichopus angulatus* (Percheron) are known as far north as Alamos in southern Sonora.

The most widely distributed species are *P. punctiger* and *P. interstitialis* Esch. *P. punctiger* ranges from northern Argentina (Bruch 1942) and Uruguay (Reyes-Castillo, 1970) to Tamaulipas, Mexico. It has been recorded from every Central American country except Belize (Reyes-Castillo 1973), but I have collected it there near Belmopan. Reyes-Castillo (1973) lists its Caribbean distribution as Trinidad, Jamaica, and Cuba, to which I add Grenada.

P. interstitialis ranges from Argentina to northern Veracruz, Mexico (Reyes-Castillo 1970). It has been recorded from every Central American country except Costa Rica (Reyes-Castillo 1973), but I have collected it there near Cañas, Guanacaste. Its Caribbean distribution includes Trinidad, Grenada, Jamaica, Cuba, and Isle of Pines (Reyes-Castillo 1973).

The distribution of many New World Passalidae is detailed in Reyes-Castillo (1970, 1973). I here add 2 new Peruvian records, *Passalus spinifer* Percheron and *Spasalus crenatus* (MacLeay), both from Tingo Maria, Huánuco Dept.

Passalids are not found in regions of prolonged cool temperatures such as occur at latitudes greater than 45° or on tropical mountains above 3500 m. The number of species and density of individuals decrease as these extremes are approached. Only 2 species are found in north temperate regions where freezing temperatures and snow occur: *Cylindrocaulus patalis* Fairm. of Japan and *Odontotaenius disjunctus* of the eastern United States and Canada.

In the neotropical mountains, only a few species of Passalidae occur at or above 2800 m. Most of these belong to the tribe Proculini (table 1). The only New World Passalini known from above 2200 m are a new species of *Passalus (Pertinax)* collected by me at 2250 m and by Reyes-Castillo, Woodruff, and Pope at 2800 m on the Sierra Talamanca in Costa Rica; an undescribed species of *Passalus (Pertinax)* found by me at 2750 m in Ecuador; and *Passalus incertus* Percheron collected by R. Wilkerson at 3000 m on Cerro de Munchique, Colombia.

In Peru (Tingo María region), I did not encounter passalids above aproximately 2500 m even though areas examined contained many apparently suitable logs. In Costa Rica on the Cerro de la Muerte of the Sierra Talamanca, Reyes-Castillo and I examined 60 to 80 logs in an oak forest above 2900 m without finding passalids. At 3000 m, the mean annual temperature (1962) was 10.8°C, the lowest temperature of the year (1963) was 00.0°C, and the highest was 24.5°C (Scott 1966).

Passalids may be loosely grouped into lowland and highland species. *P. punctiger* and *P. interstitialis* typify the lowland distribution. They are commonly found in lowlands on both sides of the central mountain ranges of Central America and Mexico below 1500 m and present a typical Neotropical distribution in the sense of Halffter (1964). Many highland species have restricted ranges and some (e.g. *Oileus nonstriatus* (Dibb) of the Sierra Madre Oriental of Mexico) have reduced wings.

Passalids occur most commonly in moist forests. Species and individuals are abundant in tropical rain forests (near Tingo Maria, Peru, 1 of every 3 or 4 logs contained passalids) and quite numerous in montane forests such as the cloud forests, pine forests, and pine-oak forests of Mesoamerica. They are less abundant in the drier, tropical deciduous forests; for example, near Cañas, Costa Rica, only 6 of 150 to 200 logs contained passalids. A few species occur in savanna (Reyes-Castillo 1970). *Odontotaenius disjunctus* inhabits northern temperate deciduous forests, including the relatively dry turkey-oak sandhills of north central Florida. One species, *Ptichopus angulatus*, is found in desert and forest regions associated with leaf-cutter ants (Hendrichs and Reyes-Castillo 1963).

Passalids are found in moist, decomposing plant material. Though I have found adults in dry rotting logs, I have encountered juvenile stages only in moist conditions. Gray (1946) showed in the laboratory that pupae of *O. disjunctus* would not reach adulthood at relative humidities below 92% and that eggs would develop only in direct contact with water. Passalids are not common where flooding is frequent, such as along some river courses.

The commonest microhabitat of passalids is a rotting log in intermediate stages of decay (standing trunks as well as fallen ones). I found a species of *Spasalus* (near *S. crenatus* Macleay) at a height of 7 m in a standing trunk near Iquitos, Peru. D. Minnick has informed me that he collected a group of

Table 1. Species of Proculini collected at or above 2800 m elevation.

SPECIES	LOCATION	SOURCE
Chondrocephalus granulifrons (Bates)	to 3300 m in pine forest GUATEMALA	Reyes-Castillo 1970
Petrejoides n. sp.	to 3270 m in pine forest Cuchumatan Mts. GUATEMALA	J. Schuster
Ogyges laevissimus (Kaup)	to 3000 m on Volcan Agua GUATEMALA	Reyes-Castillo, pers. comm. 1976
Pseudacanthus spp.	to 3000 m in southern MEXICO	Reyes-Castillo 1970
Publius crassus (Smith)	to 3000 m	Reyes-Castillo 1970
Veturius sp.	at 3000 m on Cerro de Munchique, COLOMBIA	R. Wilkerson, pers. comm. 1977
Ogyges laevior (Kaup)	to 2920 m Cuchumatan Mts. GUATEMALA	J. Schuster
Odontotaenius striatulus (Dibb)[1]	at 2900 m ECUADOR	Reyes-Castillo 1970
Petrejoides recticornis (Burmeister)	at 2860 m MEXICO	Reyes-Castillo 1970
Chondrocephalus n. sp.	to 2850 m Cuchumatan Mts. GUATEMALA	J. Schuster
Petrejoides jalapensis (Bates)	at 2800 m MEXICO	Reyes-Castillo 1970
Spurius depressifrons (Bates)	at 2800 m MEXICO	Reyes-Castillo 1976b
Spurius dichotomus Zang	at 2800 m MEXICO	Reyes-Castillo 1976b
Undulifer incisus Truqui	at 2800 m MEXICO	Reyes-Castillo 1970
Vindex agnoscendus (Percheron)	at 2800 m MEXICO	Reyes-Castillo 1970
Vindex sculptilis Bates	to 2850 m Cuchumatan Mts. GUATEMALA	J. Schuster

[1]synonymous with *O. striatopunctatus* (Percheron)?

O. disjunctus more than 6 m above the ground in a standing trunk in Marion Co., Florida.

Tunnels may occur in one area of a log and not in another. I observed that tunnels of the *Spasalus* sp. mentioned above did not cross certain fungus lines in the wood (probably an ascomycete). They occurred primarily in areas through which the fungus had apparently already penetrated.

Most species occur in dicotyledenous wood, though many occur in conifers (e.g. *Pinus, Araucaria*) and a few are found in palms (Reyes-Castillo 1970). Some species are more restricted than others; for example, *O. disjunctus* is found in dicotyledenous wood but seldom in pine (Savely 1939), whereas *O. striatopunctatus* is commonly found in both. Up to 10 species have been encountered in a single log (Luederwaldt 1931). Flatter species tend to be found under bark (e.g., *Passalus interstitialis*), more convex species deeper in the log (e.g. *P. convexus*).

A few Passalidae occur in other microhabitats. *Passalus punctiger* has been found under cow manure in Brazil, and larvae, pupae and adults of *P. dubitans* (Kuwert) have been collected under epiphytic bromeliads in Brazil (Luederwaldt 1931). J. G. Edwards and R. Mains (pers. comm., 1972) collected Passalidae under stones in the Yucatan Peninsula. *Ptichopus angulatus* is commonly found in the detritus associated with nests of the leaf-cutter ant, *Atta mexicana*, both in the wet forest regions and in desert regions of Mexico (Hendrichs and Reyes-Castillo 1963; Reyes-Castillo 1970). In a desert of Hidalgo, Mexico, Reyes-Castillo and I found passalid larvae and adults together 30 cm deep in the detritus of such an ant nest. Despite general dryness this nest section had visibly greater moisture, and the detritus was well packed so that passalid tunnels were easily visible as we excavated.

In Peru, during 1970 and 1971, I found evidence of passalids in a particularly unusual habitat: limestone caves. Near the town of Tingo Maria is a large cave, known locally as the "Cueva de las Lechuzas". Its mouth is about 18 m in diameter and the first chamber is about 30 m wide. Within it lives a large colony of oilbirds, *Steatornis caripensis* Humboldt. These birds feed on fruits, especially of a palm *(Bactris gasipaes* H.B.K.), which they bring into the cave (Dourojeanni and Tovar 1972). The seeds are dropped on the floor and these, as well as excrement from the birds and from bats, provide nutrients for a large arthropod fauna within the cave. The most apparent arthropods are a large black tenebrionid beetle, a small lygaeid bug, and a large cockroach of the genus *Blaberus*. Amid the insect remains which litter the cave floor, I observed many pieces of passalid exoskeletons, especially elytra. They appeared to be most common about 45 m from the cave mouth, but occurred as far back as 200 m from the entrance. In a 360 cm^2 area 20 m from the entrance, I counted remains of 19 individual passalid beetles. Though I saw no living passalids in the cave, Dourojeanni (pers. comm., 1973) noted live passalids, adults and larvae, there in 1961, and suggested that they fed on the decomposing seeds brought in by the birds (Dourojeanni and Tovar 1972).

I noted passalid remains in 3 other caves in which oilbirds live or formerly lived in that region of Peru. However, I found similar remains under an overhanging cliff (margin of cliff extended about 3 m beyond the base and formed a grotto about 9 m wide), and in a small cave (entrance

diameter 3 m). In neither were there oilbirds or evidence, such as palm seeds on the floors, that oilbirds had ever occupied them. Both sites are located in southern San Martin province near the village of Aspusana. In no case did I find an entire passalid or a living beetle, only pieces. Most of the insect remains in the cave were concentrated under a small ledge about 50 cm above the cave floor. Seventy-five percent (57 individuals) of the arthropods represented were passalids. There were remains of 32 individuals of *Passalus interruptus* as well as remains of 2 other *Passalus* species and a *Veturius* species, probably *V. platyrhinus* (Westwood). The only other insects represented by remains of more than one individual were 7 ponerine ants and 4 *Rhinostomus barbirostris* (Fabricius), a large curculionid. *P. interruptus* and *V. platyrhinus* are among the commonest passalids collected in this region of Peru. Since there was very little, if any, decomposing plant matter in this cave, I am forced to conclude that the beetles were brought into it, perhaps by bats or rodents, and the pieces were then collected, possibly by the latter, under the ledge. The high proportion of passalid parts, predominantly elytra, might be explained by the fact that they are quite glossy and may be more attractive to acquisitive rodents than other insect pieces they eat or find. Perhaps such collecting also contributed to the passalid remains in the oilbird caves.

In summary, most species of Passalidae are tropical and live in warm, moist habitats associated with decomposing plant matter, usually rotting wood. Few species are found in temperate regions, above 2800 m altitude, or in deserts. The most widespread New World species inhabit the tropical lowlands, usually below 1500 m elevation.

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